

# Urocyon cinereoargenteus. By Erik K. Fritzell and Kurt J. Haroldson

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## Urocyon Baird, 1858

*Urocyon* Baird, 1858:12. Type species *Canis virginianus* Erxleben (= *Canis virginianus* Schreber). Proposed as subgenus of *Vulpes*.

**CONTEXT AND CONTENT.** Order Carnivora, Family Canidae, Subfamily Caninae. Two recent species, *Urocyon cinereoargenteus* and *U. littoralis*, are usually recognized; *U. littoralis* is a smaller insular form and may not deserve specific status. Two recent revisions of the family have suggested that *Urocyon* be included in *Vulpes* (Clutton-Brock et al., 1976) or *Canis* (*Vulpes*) (Van Gelder, 1978). We have retained the earlier nomenclature based solely on its persistence and familiarity.

## Urocyon cinereoargenteus Schreber, 1775

Gray Fox

*Canis cinereo argenteus* Schreber, 1775:pl. 92. Type locality eastern North America.

*Canis virginianus* Schreber, 1775:585. Type locality Carolina and warmer parts of North America.

[*Vulpes*] *Pensylvanicus* Boddaert, 1784:97. Type locality Pennsylvania.

*Canis nigrirostris* Lichtenstein, 1850:106. Type locality Real Arriba, Estado Mexico.

*Urocyon californicus* Merriam, 1899:103. Elevated *californicus* Mearns to species status.

*Urocyon parvidens* Miller, 1899:276. Type locality Mérida, Yucatan.

*Urocyon guatemalae* Miller, 1899:278. Type locality Nentón, Huehuetenango, Guatemala.

**CONTEXT AND CONTENT.** Sixteen subspecies are recognized as follows:

*U. c. borealis* Merriam, 1903:74. Type locality Marlboro, Cheshire Co., New Hampshire.

*U. c. californicus* Mearns, 1897:459. Type locality Tahquitz Valley, San Jacinto Mts., Riverside Co., California.

*U. c. cinereoargenteus* Schreber, 1775, see above (*virginianus* Schreber and *pensylvanicus* Boddaert are synonyms).

*U. c. costaricensis* Goodwin, 1938:2. Type locality Sabanilla de Pirris, Prov. San José, Costa Rica.

*U. c. floridanus* Rhoads, 1895:42. Type locality Tarpon Springs, Hillsboro Co., Florida.

*U. c. fraterculus* Elliot, 1896:80. Type locality San Felipe, Yucatan (*parvidens* Miller a synonym).

*U. c. furvus* Allen and Barbour, 1923:266. Type locality Balboa, Canal Zone.

*U. c. guatemalae* Miller, 1899:278, see above.

*U. c. madrensis* Burr and Hooper, 1941:4. Type locality Carimechi, Rio Mayo, Chihuahua.

*U. c. nigrirostris* Lichtenstein, 1850, see above.

*U. c. ocythous* Bangs, 1899:43. Type locality Platteville, Grant Co., Wisconsin.

*U. c. orinomus* Goldman, 1938:497. Type locality Orizaba, Veracruz.

*U. c. peninsularis* Huey, 1928:203. Type locality San Ignacio, Baja California.

*U. c. scottii* Mearns, 1891:236. Type locality Pinal Co., Arizona (*texensis* Mearns and *inoensis* Elliot are synonyms).

*U. c. townsendi* Merriam, 1899:103. Type locality Shasta Co., California (*sequoiensis* Dixon a synonym).

*U. c. venezuelae* Allen, 1911:259. Type locality El Tocuyo, Lara, Venezuela.

**DIAGNOSIS.** Members of the genus *Urocyon* can be distinguished readily from most other canids by their grizzled upper-

parts, cinnamon to buff neck and underparts, and black-tipped tail with dorsal median mane of coarse, black-tipped hairs (Fig. 1). The skull (Fig. 2) can be separated from those of other North American canids by conspicuous, widely separated temporal ridges that approach each other posteriorly to produce a lyrate- or U-shaped form (also found in *Otocyon*). The supraorbital crest is slightly downcurved and has a distinct concave depression on the upper surface. The temporals are roughened below the temporal ridges. The dentary has a prominent "step" or notch near the posterior ventral border (also found in *Otocyon* and *Nyctereutes*). *Urocyon cinereoargenteus* is approximately 20% larger in major body dimensions than *U. littoralis*. Grinnell et al. (1937) provided detailed comparisons. The bones of the post-cranial skeleton are more massive in *U. littoralis* and have more accentuated rugosities and muscle scars (Hildebrand, 1954).

**GENERAL CHARACTERS.** The grizzled appearance of the back and sides of *Urocyon* results from individual guard hairs being banded with white, gray, and black. A predominance of black-tipped hairs near the middle of the back forms a dark longitudinal stripe which extends into a conspicuous black mane of coarse hair on the top of the black-tipped tail. Portions of the neck, sides, and limbs are cinnamon-rufous. White shows on the ears, throat, chest, belly, and hind legs. Black, white, and rufous facial markings are distinctive. Underfur is mostly buff and gray.

External body measurements range as follows: total length, 800 to 1,125 mm; tail length, 275 to 443 mm; hindfoot length, 100 to 150 mm (Hall, 1981). Adult weights range from about 3 to 7 kg; males are slightly larger than females (Grinnell et al., 1937; Jackson, 1961; Sullivan, 1956). Condylbasal length of the skull ranges from 110 to 130 mm (Hall, 1981). Additional body and cranial measurements are presented by Clutton-Brock et al. (1976), Grinnell et al. (1937), Jones (1964), and Paradiso (1969).

**DISTRIBUTION.** Gray foxes inhabit wooded, brushy, and rocky habitats from extreme southern Canada to northern Venezuela and Colombia, excluding portions of mountainous northwestern United States, the Great Plains, and eastern Central America (Fig. 3). During the last 50 years their range has expanded into areas formerly unoccupied or into areas where the species had been extirpated. Noteworthy regions of range extension include: New England (Godin, 1977; Palmer, 1956), Ontario (Downing, 1946; Peterson et al., 1953), Michigan (Allen, 1940; Ozoga and Verme, 1966), Minnesota (Timm, 1975), Iowa (Bowles, 1975), Manitoba (Sutton, 1958), North Dakota (Schantz, 1950),



FIGURE 1. An adult gray fox (*Urocyon cinereoargenteus*) (photo from Kansas Fish and Game).

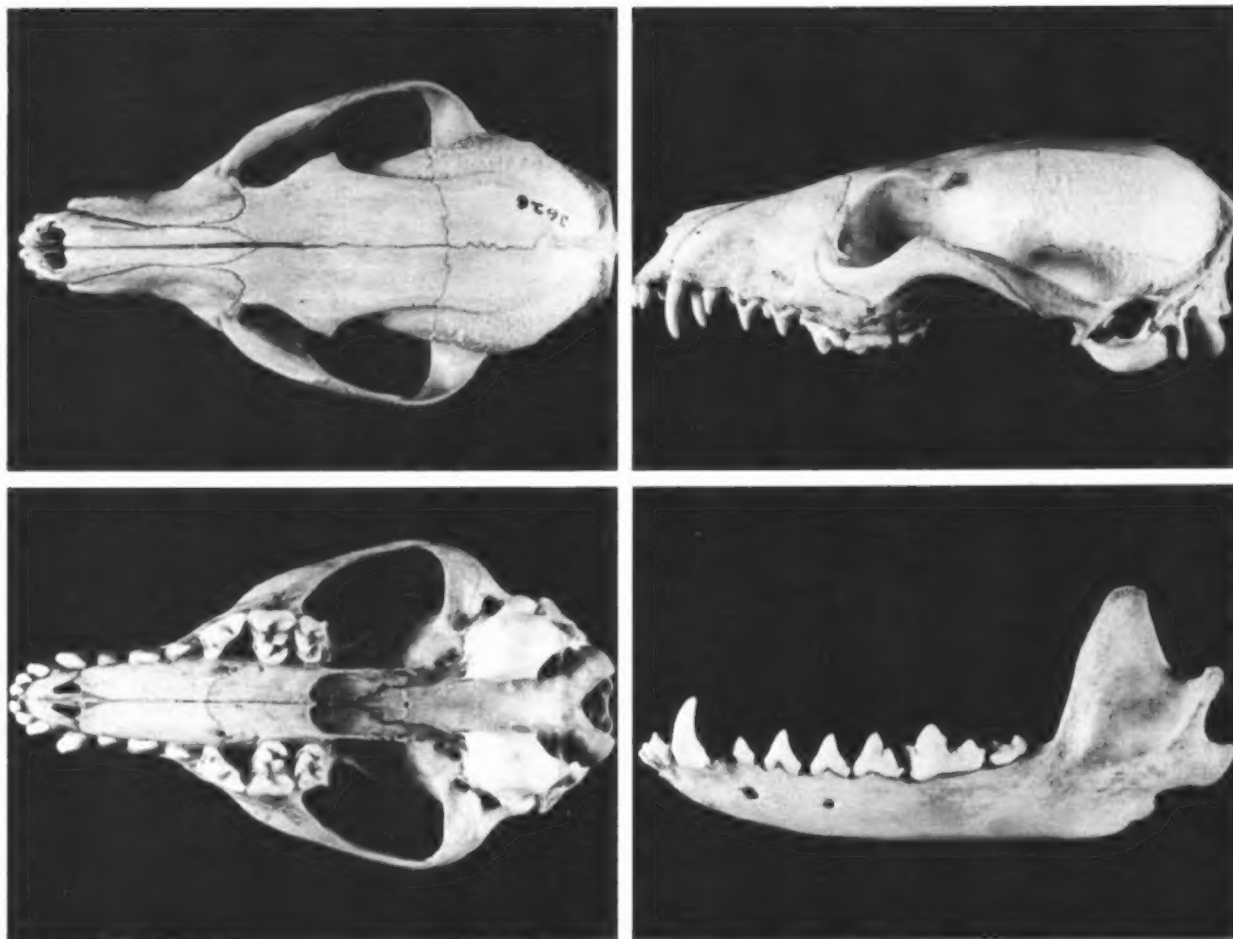


FIGURE 2. Views of skull and mandible of *Urocyon cinereoargenteus* (Univ. Missouri 3628). Greatest length of skull is 121.0 mm.

South Dakota (Jones and Henderson, 1963), Nebraska (Jones, 1964), Kansas (Choate and Krause, 1974), Oklahoma (Halloran and Glass, 1959; Schendel, 1942), and Utah (Durrant et al., 1955). An extralimital record resulted from a specimen trapped near Lake Athabasca, Alberta (Banfield, 1974). Archeological evidence suggested that *U. cinereoargenteus* arrived on Martha's Vineyard, Massachusetts, about 1,500 years ago, but was extirpated when Europeans arrived in the mid-1500's (Waters, 1967).

**FOSSIL RECORD.** Kurtén and Anderson (1980) summarized the fossil record as follows. The genus *Urocyon* has been present in North America since the Hemphillian land mammal age (Pliocene). The extinct *U. progressus* occurred throughout most of the Blancan age; it is found in Rexroad, Red Light, and possibly Broadwater local faunas. *U. cinereoargenteus* has been found at almost 40 Pleistocene localities, the oldest of which date back to the late Irvingtonian (Cumberland, Conard Fissure, and Coleman IIA local faunas) or possibly the early Irvingtonian (Port Kennedy local fauna). Sangamonian interglacial records include the Cedazo, Haile VIIIA, and Reddick local faunas. During the Wisconsin glaciation the gray fox was widely distributed from California to Florida and reached its northern limit in Pennsylvania. *U. littoralis* evidently reached the Channel Islands off California in the late Pleistocene (Stock, 1943).

**FORM AND FUNCTION.** Guard hairs range from 50 to 70 mm; hair scales are imbricate with edges acuminate proximally, gradually changing to crenate medially and flattened distally. Light gray underfur is approximately 30 to 40 mm in length; scales are coronal with edges dentate (Adorjan and Kolenosky, 1969); additional descriptions and keys to hair are included in Brown (1942) and Mayer (1952). A single annual molt extends from summer through autumn (Grinnell et al., 1937). Hair slope patterns, arrangement of body hairs and vibrissae, mastology, and tail gland characteristics were described in detail by Hildebrand (1952a,

1954). *U. cinereoargenteus* has the largest tail gland of the North American canids, extending one-third to one-half the length of the tail (Hildebrand, 1952a; Seton, 1923). Six mammae are usually present.

There are 42 teeth (i 3/3, c 1/1, p 4/4, m 2/3). Dental anomalies have been described (Easterla, 1968; Hall, 1940; Pavlinov, 1975). Body proportions and post-cranial skeleton were described and compared to those of other canids by Hildebrand (1952b, 1954). He suggested that *U. cinereoargenteus* is able to rotate the forearm as much or more than any other canid, perhaps as an adaptation for climbing. Skeletal measurements were also reported by Rohde (1966); males were found to have longer pelves, longer and wider scapulae, more massive limb bones, and longer calcanea than females of corresponding age classes. An *os clitoridis* is present (Hildebrand, 1954). Comparative studies of the calcanea (Stains, 1975), brain (Radinsky, 1969, 1973), adrenals (Heinrich, 1972), and ovaries (Mossman and Duke, 1973) include descriptions of these organs in *Urocyon*. Immunological and electrophoretic data relating to canid taxonomy were reported by Seal (1975). Trehalase activity in kidney tissue from a gray fox measured 14 micromoles glucose produced per gram of tissue (Van Handel, 1969).

A dwarf, brachycephalic gray fox was described by Stone et al. (1971).

**ONTOGENY AND REPRODUCTION.** The breeding season of gray foxes varies geographically. Wood (1958) collected pregnant females in early January but suggested early February as the peak breeding period in southern Georgia; no females were in estrus later than March. Mating dates of gray foxes from New York have been estimated by Layne and McKeon (1956a) and Sheldon (1949); breeding activity extended from late January to May and peaked in March. Breeding activity occurs from late January through February in southern Illinois (Layne, 1958) and

from late January through March in Wisconsin (Richards and Hine, 1953; Root, 1981). The peak of mating of gray foxes in Alabama is in February (Sullivan, 1956). Where *U. cinereoargenteus* and *Vulpes vulpes* are sympatric, gray foxes breed 2 to 4 weeks later than do red foxes (Layne and McKeon, 1956a; Richards and Hine, 1953; Sheldon, 1949). The gestation period of gray foxes is unknown; however, it has been reported to be 63 days (Asdell, 1964; Grinnell et al., 1937) or 53 days, as in *Vulpes vulpes* (Sheldon, 1949; Wood, 1958).

The annual reproductive cycle of males has been described by the use of epididymal smears (Layne, 1958; Root, 1981; Wood, 1958), testicular and epididymal smears (Sullivan, 1956), and histological techniques (Follmann, 1978). In those studies, males were fertile (with abundant spermatozoa in the epididymides) during periods bracketing the respective breeding seasons of females. Therefore, males become fertile earlier and remain fertile longer than females.

The annual reproductive cycle of males in southern Illinois was described by Follmann (1978). Numbers of spermatogonia began increasing in September, peaked in January, and gradually declined until April. Primary spermatocytes were present in the testes throughout the year but in reduced numbers during the summer, suggesting some spermatogenic activity year-round. Spermatids first formed in November, reached peak numbers in January, and declined until March. Spermatozoa were present in the testes from November to April with their peak abundance in March. Epididymides, however, contained spermatozoa from October through June suggesting that full spermatogenesis had begun as early as September; spermatozoa were abundant in the epididymides between December and March.

Most females are sexually mature at 10 months of age. Ten of 54 yearlings examined from Wisconsin were barren (Root, 1981). Of 78 yearlings from Georgia examined by Wood (1958), six did not show signs of sexual maturity. In that study, no difference was detected between the times of breeding of 56 yearlings and 44 older females. Layne (1958), however, suggested that some yearlings may reach puberty too late for successful mating. He collected a barren female in mid-June whose reproductive tract and teats were virginal, but whose ovaries contained well developed corpora lutea.

Level of spermatogenesis during the breeding season is not influenced by age or previous spermatogenic activity (Follmann, 1978). Testes of adult and yearling males had equivalent numbers of spermatogonia, primary spermatocytes, spermatids, and spermatozoa throughout the reproductive cycle. Testes of two juvenile foxes collected in July were similar to those of adults, including the presence of primary spermatocytes, indicating that testicular activity begins about 4 months after birth. Fewer spermatozoa in epididymides of yearling males than in adult males during January and February, however, suggested to Follmann that yearlings began spermatogenesis later than adults or that testes of yearlings reached full activity slower than those of adults.

The synthetic estrogen, diethylstilbestrol (DES), may inhibit or delay ovulation in gray foxes. In a field test, females consuming baits treated with 50 mg of DES and a physiological marker failed to ovulate; but the results, as the authors indicated, were equivocal (Oleyar and McGinnes, 1974).

Mean litter size of gray foxes based on counts of fetuses and placental scars from seven studies ( $n = 304$ ) was 3.8 young per female (Layne, 1958; Layne and McKeon, 1956a; Lord 1961a; Richards and Hine, 1953; Root, 1981; Sheldon, 1949; Sullivan, 1956). Four fetuses or scars are most common, but 1 to 7 have been recorded. Litter sizes did not vary among foxes 1.5 to 4.5 years old (Root, 1981). Primary sex ratios do not differ significantly from 1:1. Of 102 fetuses examined in three studies, 54 were male and 48 were female (Layne and McKeon, 1956a; Sheldon, 1949; Wood, 1958).

Data describing development of gray foxes are meager and often anecdotal (e.g., Taylor, 1943); however, several methods of estimating age have been described. Wood (1958) reported on tooth wear, closure of skull sutures, vomer and baculum development, and weight changes based on 22 individuals of known and 375 of unknown age. He distinguished five distinct age groups by the amount of wear on the canines of M1. The basisphenoid-presphenoid suture closed during month 10 or 11. The vomer was fully developed and continuous with the presphenoid at about 24 months. He found no clear-cut differences in baculum weights of juveniles and adults, contrary to Petrides (1950). The changes in weight (g) of juvenile gray foxes were as follows: at birth, 86; 11 days, 129; 19 days, 169; 23 days, 234; 30 days, 249; 51 days, 588; 78 days, 1,200; 90 days, 1,500; 120 days, 2,000; 150 days, 2,500; 180 days, 3,400; 210 days, 3,700 ("adult-sized"). When using eye



FIGURE 3. The geographic range of the gray fox (*Urocyon cinereoargenteus*). Modified from Hall (1981) and Hershkovitz (1953).

lens weights to distinguish between adult and juvenile foxes, Lord (1961b) found 90% agreement with Wood's methods. Distal epiphyses of the radius and ulna ossified between 8 and 9 months of age (Sullivan and Haugen, 1956). Sequences of eruption of cheek-teeth were described by Slaughter et al. (1974).

Cementum annuli counts, amounts of tooth wear, and eye lens weights were compared among 211 gray foxes from Alabama and Georgia (Nicholson and Hill, 1981). In that study, three observers independently estimated age from annuli and tooth wear categories. Ages assigned by tooth wear were highly variable among observers; counts of cementum annuli were believed to be the most accurate aging method; but eye lens weights separated most juveniles and adults. Root (1981) reported a subjective aging method based on the examination of roots of upper canines, apical foramina, widths of pulp cavities, and cementum annuli.

**ECOLOGY.** No carnivore in eastern North America is more closely associated with the deciduous forest than the gray fox (Hall, 1981). In Wisconsin, gray foxes were most abundant near brush covered bluffs where woodland and farmland were well interspersed (Petersen et al., 1977; Richards and Hine, 1953). Likewise, woodland/farmland edge provided the best gray fox habitat in southern Georgia (Wood et al., 1958), Virginia (Carey et al., 1978), and the post oak woodlands of Texas (Wood, 1952). In western North America, gray foxes favored brushy vegetation in association with rugged, broken terrain (Grinnell et al., 1937; Hardy, 1945; Johnson et al., 1948; Leopold, 1959; Nelson, 1930). Gray foxes in California are most abundant at elevations of 1,150 to 1,525 m (Grinnell et al., 1937; Johnson et al., 1948).

Several studies using radio-telemetry provided detailed information on habitat use by gray foxes. Follmann (1973), in southern Illinois, and Trapp (1978), in southwest Utah, found that early old fields were used more than expected relative to habitat availability, agricultural and brushy habitats were used less than expected, and woodlands were used in proportion to that expected. Gray foxes in California selected against agricultural habitats and in favor of woodlands when present within their home range; otherwise old fields were used more than expected (Fuller, 1978). Seasonally, old fields were used most during summer or fall when fruits and insects were abundant (Follmann, 1973; Yearsley and Samuel, 1980). Gray foxes used woodlands more during the day than at night throughout the year (Follmann, 1973; Yearsley and Samuel, 1980).

Gray foxes use dens at any time of the year, but most use

occurs during the whelping season. Dens are usually located in brushy or wooded habitats and are less conspicuous than dens of *Vulpes vulpes* (Faylor, 1969; Layne and McKeon, 1956; Nicholson and Hill, 1981; Sullivan, 1956). In Wisconsin, most dens of gray foxes were situated on east, southeast, or south-facing slopes (Richards and Hine, 1953). Hollow logs or trees, rock outcrops, underground burrows, cavities under rocks, abandoned buildings, piles of wood, sawdust, or brush serve as suitable den sites for gray foxes. Most underground dens are probably abandoned dens of other animals (Schmeltz and Whitaker, 1977), which do not require an extensive amount of excavation by foxes (Sullivan, 1956). Grinnell et al. (1937) described a whelping den 7.6 m above the ground in a hollow tree. Diurnal retreats of gray foxes in southwest Utah were usually above ground in the shade of boulders, trees, or cliffs (Trapp, 1978). In California and east-central Alabama, daytime resting sites were located in areas of dense vegetation (Hallberg and Trapp, in press; Nicholson and Hill, 1981). No difference was observed in the habitats of summer and winter daytime resting areas (Nicholson and Hill, 1981).

As determined by radio-telemetry, average home-range size varies according to sex and geographic location as follows: 97 ha for males ( $n = 3$ ) and 75 ha for a female in West Virginia (Yearsley and Samuel, 1980); 136 ha for males ( $n = 2$ ) and 107 ha for females ( $n = 4$ ) in southern Illinois (Follmann, 1973); 653 ha for males ( $n = 5$ ) and 626 ha for females ( $n = 15$ ) in east-central Alabama (Nicholson and Hill, 1981); 102 ha for males ( $n = 4$ ) and 113 ha for females ( $n = 4$ ) in southwest Utah (Trapp, 1978); 129 ha for males ( $n = 2$ ) and females ( $n = 2$ ) (Hallberg and Trapp, 1982) and 122 ha for females ( $n = 4$ ) in California (Fuller, 1978). Home range size increases for both sexes in late fall and winter; during the whelping period it decreases for females but peaks for males (Follmann, 1973; Nicholson and Hill, 1981). Home ranges are typically elongate (Follmann, 1973; Montague, 1975; Trapp, 1978). Home-range diameters estimated without the aid of radio-telemetry varied from 0.4 to 3.2 km (Lord, 1961a; Richards and Hine, 1953).

Juvenile gray foxes have dispersed as far as 84 km from their natal area (Sheldon, 1953). Of nine juveniles (three males, six females) radio-marked in east-central Alabama, only the males dispersed. Females made exploratory movements as far as 3 km from their natal area but always returned (Nicholson and Hill, 1981). In contrast, Follmann (1973) radio-tagged five subadult gray foxes (two males, three females) which exhibited no long range dispersal.

Based on the age ratios of gray fox populations trapped during two consecutive years in northern Florida, Lord (1961a) estimated that 43 to 47% of the foxes born died in their first 7 months, and that 61 to 64% of the adults died annually. In southern Georgia, annual mortality rates were 50% for a juvenile's first summer, 90% for the first winter, and 50% for adults (Wood, 1958). Michod and Anderson (1980) estimated rate of increase and age specific longevities for the same Georgia fox population using Wood's (1958) data. In a sample of 435 gray foxes collected in Georgia, 89.4% were less than 2 years old (Wood, 1958). During fall and winter, 58% of 43 females trapped in Ohio and 52% of 54 females trapped in Illinois were juveniles (Layne, 1958; Petrides, 1950). Yearlings constituted 80% of the 107 foxes trapped in Virginia from May through August (Carey et al., 1978). Nevertheless, a few gray foxes may reach 14 to 15 years of age in the wild (Seton, 1929).

The adult sex ratio does not usually vary significantly from 50:50 (Carey et al., 1978; Layne, 1958; Petrides, 1950; Richards and Hine, 1953; Root, 1981; Wood, 1958). One exception was reported in New York, where 59% of 1,132 adults trapped were male (Layne and McKeon, 1956a).

Estimated densities of gray foxes vary from 1.2 to 2.1 per km<sup>2</sup>, depending on location, season, and method of estimation (Errington, 1933; Gier, 1948; Lord, 1961a; Trapp, 1978). Grinnell et al. (1937) reported 15 gray foxes being trapped within a 260 ha area during the last half of February (mating season) in California. Based on bounty data, Richmond (1952) found that the gray fox population in Pennsylvania was highest during years in which January, February, and March were wetter and warmer than average and lowest during years when the same months were colder and drier than normal.

Dyson (1965) maintained captive gray foxes on diets of natural and prepared foods equalling 3.8% of their body weight (daily feedings are assumed but not specified). Specific foods consumed in the wild vary among locations and seasons. Mammals compose the greatest portion of winter gray fox diets in the eastern and

central U.S. Rabbits (*Sylvilagus*) are the principal prey but rodents (especially *Microtus*, *Peromyscus*, *Neotoma*, and *Sigmodon*) are also important, as determined by studies of food habits in Florida, Georgia, and South Carolina (Wood et al., 1958), Iowa (Scott, 1955), Massachusetts (MacGregor, 1942), Minnesota (Hatfield, 1939), Missouri (Korschgen, 1957), eastern Texas (Wood, 1954), Virginia (Nelson 1933), West Virginia (Glover, 1949), and Wisconsin (Errington, 1935). Although mammalian prey is important in the diet throughout the remainder of the year in these regions, invertebrates (particularly orthopterans) often predominate during summer (Korschgen, 1957; Wood et al., 1958) or autumn (Kozicky, 1943). Plant foods, especially persimmon (*Diospyros virginiana*), grapes (*Vitis*), apples (*Malus*), and corn (*Zea mays*), also increase in importance during autumn (Korschgen, 1957; Llewellyn and Uhler, 1952) and may form 70% of the diet by volume (Pils and Klimstra, 1975). Other foods less commonly eaten by gray foxes throughout the eastern and central U.S. include birds (including poultry), squirrels (*Sciurus*), opossum (*Didelphis virginianus*), and deer (*Odocoileus*) carrion. However, McKinnerney (1978) noted that gray foxes in the Chihuahuan Desert only scavenged on fresh (1- or 2-day-old) carrion. In southwest Utah, fruits were the most important food, followed by mammals (mainly *Odocoileus*, *Thomomys*, *Peromyscus*, and *Neotoma*) and arthropods, primarily orthopterans and coleopterans (Trapp, 1978). Seasonally, arthropods dominated the summer diet and fruits dominated the fall and winter diets, with *Opuntia* fruits being most important in the fall and *Juniperus* in the winter and early spring. Juniper berries were also the most frequently eaten food during spring and summer in Arizona (Small, 1971). Mammalian prey formed the largest portion of the diets of gray foxes in California (Fitch, 1948; Grinnell et al., 1937).

Gray foxes host at least 15 species of fleas, 2 species of lice, 9 species of ticks, 2 species of chiggers, and 7 species of mites (Coultrip et al., 1973; Eads and Menzies, 1950; Whitaker and Goff, 1979; Wilson and Baker, 1972). Unlike the red fox, gray foxes are highly resistant to infestation by sarcoptic mange mites (*Sarcoptes scabiei*); two of five adults became only mildly infested and quickly recovered when experimentally contaminated with "thousands" of mange mites, whereas red foxes subjected to similar treatment died as a result (Stone et al., 1972). Gray foxes also host at least 5 species of trematodes, 8 species of cestodes, 17 species of nematodes, and 2 species of acanthocephalans (Buechner, 1944; Chandler and Melvin, 1951; Erickson, 1944; Miller and Harkema, 1968). Diseases known to infect gray foxes include rabies, canine distemper, St. Louis encephalitis, tularemia, listeriosis, leptospirosis, histoplasmosis, toxoplasmosis, Q fever, and Tyzzer's disease (Davis et al., 1970; Emmons and Lennette, 1967; Enright et al., 1971; Marchiondo et al., 1976; Stanley et al., 1978).

Gray foxes have been examined for the accumulation of mercury in their hair (Cumbie and Jenkins, 1975) and for the effects of exposure to acute gamma radiation (Golley et al., 1965), tear gas (Andrews, 1964), and vertebrate pesticides (Bell and Dimmick, 1975; Wade, 1977).

After analyzing Pennsylvania bounty records, Latham (1952) thought that population levels of foxes (both red and gray) were inversely related to population levels of weasels (*Mustela* spp.), and suggested that foxes were capable of reducing weasel populations. The weasel population on a Virginia turkey farm erupted after gray foxes were trapped out, but levels of skunks (*Mephitis mephitis*), opossums, and raccoons (*Procyon lotor*) remained unchanged. The weasel population later dropped as the foxes became reestablished (Hensley and Fisher, 1975). Sympatric ringtails (*Bassariscus astutus*) and gray foxes in southwest Utah differed in habitat use patterns and food habits (Trapp, 1978). In southern Illinois, Follmann (1973) found greater overlap in home ranges between red and gray foxes than overlap in home ranges within either species. He believed that as farmland reverted through the secondary successional stages, gray foxes would gradually replace red foxes. In New York, Saggese and Tullar (1974) reported possible predation by a gray fox on a red fox pup. Dudley (1976) described an agonistic encounter between a bobcat (*Lynx rufus*) and two gray foxes in New Mexico.

Undoubtedly the most important predator of the gray fox is man. The total fur harvest of gray foxes in the U.S. increased from 26,109 animals during the 1970-71 season to 163,458 animals during the 1975-76 season, which paralleled a five-fold increase in average pelt price over the same period (Deems and Pursley, 1978). Petersen et al. (1977) estimated that nearly half of the gray fox population present on 1 October in Wisconsin was harvested annually. Other predators of gray foxes include golden eagles (*Aquila chrysaetos*) (Grinnell et al., 1937; Mollhagen et al.,



1972) and possibly coyotes (*Canis latrans*) and bobcats (Gander, 1966; Grinnell et al., 1937). Local populations of gray foxes may also be reduced by diseases, especially canine distemper (Nichelson and Hill, 1981) and rabies (Trapp and Hallberg, 1975). Weaver (1939) described a gray fox that starved as the result of an encounter with a porcupine (*Erethizon dorsatum*).

**BEHAVIOR.** Gray foxes are primarily nocturnal or crepuscular (Follmann, 1973; Grinnell et al., 1937; Hallberg and Trapp, in press; Kavanau and Ramos, 1975; Montague, 1975; Nichelson and Hill, 1981; Seton, 1929; Taylor, 1943; Trapp, 1978; Yearsley and Samuel, 1980), although local shifts in diurnal resting places are common (Hallberg and Trapp, in press; Trapp, 1978). In West Virginia and California, gray foxes were more active at night than during the day, as determined by radio-telemetry (Hallberg and Trapp, in press; Yearsley and Samuel, 1980). Likewise, in southern Illinois and California, gray foxes traveled greater distances per hour at night than during the day (Follmann, 1973; Hallberg and Trapp, in press). The average distance between a diurnal rest area and each individual nocturnal radio location of gray foxes in southwest Utah was 525 m (Trapp, 1978). Young gray foxes given instrumental control over the ambient light level in the laboratory preferred bright light after about 4 weeks of age (Kavanau et al., 1972; Kavanau et al., 1973). Adults showed a sharp drop in activity indices when illuminance dropped below 0.1 lux (50% of full moon), suggesting that their vision may be limited in dim light (Kavanau and Ramos, 1975).

Indirect observations of social organization of gray foxes, derived from radio-telemetry and relative trap success, suggest that family units, comprising an adult male and female and possibly juveniles, maintain spatially or temporally separate home ranges (Follmann, 1973; Lord, 1961a; Trapp, 1978). However, Hallberg and Trapp (in press) described the home ranges of four gray foxes (two males, two females) that occupied the same area during spring and summer.

Gray foxes are assumed to be monogamous, but conclusive evidence is lacking. Nichelson and Hill (1981) radio-tracked two mated pairs during parts of the breeding and denning seasons. They found that males foraged separately from females at night and usually returned to the den at daylight, but did not make repeated trips to the den as did the females. By 3 months of age, young accompany female parents away from the den and by 4 months of age, they begin to forage independently (Nichelson and Hill, 1981; Wood, 1958).

Fox (1969a, 1969b, 1970, 1971) compared the ontogeny of various behavior patterns between selected species of Canidae raised in captivity. Gray foxes were judged to be more social than red or arctic (*Alopex lagopus*) foxes because only they exhibited allogrooming; however, gray foxes had the least obvious facial expressions (Fox, 1970). Young gray foxes (5 to 8 weeks) frequently raised a hind leg and presented their genitalia to a conspecific in an apparent submissive or appeasement gesture (Fox, 1971; Taylor, 1943). Aggressive or playful attacks between gray foxes were directed at the cheek, where the fur is accentuated by white hair and the skin is especially thick (Fox, 1969a). Prey-killing patterns were present early in the life of gray foxes; subsequent development of play behavior suggested that play did not contribute to the organization of prey-killing patterns (Fox, 1969b).

Urine and feces apparently play a role in gray fox communication, as evidenced by deposition in conspicuous locations, such as on bare ground, on logs, rocks, and other elevated sites, or along trails (Grinnell et al., 1937; Richards and Hine, 1953; Trapp, 1978). Scats are often deposited in groups: 72% of 240 scats found in southwest Utah occurred singly and 17% occurred in groups of 2 to 8 (Trapp, 1978). Tembrock (1963) reported the principal sound frequencies of the bark of gray foxes.

Gray foxes are well known for their tree-climbing behavior. They have been observed climbing vertical, branchless tree trunks to heights of 18 m by grasping the trunk with their forefeet and pushing with their hindfeet (Bailey, 1941; Leopold, 1959; Seton, 1929; Taylor, 1943; Terres, 1939). Climbing is also accomplished by jumping from branch to branch (Grinnell et al., 1937; Seton, 1929). Trees are climbed for purposes of foraging (Grinnell et al., 1937; Gunderson, 1961), resting (Leopold, 1959; Seton, 1929; Yeager, 1938), or escape (Carr, 1945; Terres, 1939). Descent may be accomplished by backing down a vertical tree (Seton, 1929) or running headfirst down a sloping tree (Nelson, 1930; Yeager, 1938). Gray foxes in the forested eastern regions of Mexico have sharper and more recurved claws than conspecifics in more arid western regions (Goldman, 1938).

Turkowski (1971) observed an adult gray fox attempting to

decoy human intruders away from a whelping den by feigning an injured leg.

**GENETICS.** Wurster and Benirschke (1968) described the karyotype of a female to which most authors (Chiarelli, 1975; Matthey, 1973; Pizzimenti, 1971) subsequently refer. The gray fox has a diploid chromosome number of 66 with a fundamental number of 70. The autosomes include one pair of medium-size metacentrics and 31 pairs of size-graded acro- or subacrocentrics, two of which possess achromatic regions in the long arm next to the centromere. The X chromosome is the largest element and is submetacentric. The Y chromosome is the smallest element and is metacentric (Hsu and Benirschke, 1970).

An albinistic gray fox was described from New York (Shipherd and Stone, 1974). "Samson" gray foxes lacking guard hairs have been described (Grinnell et al., 1937; Root, 1981). A single report of a *Urocyon* × *Vulpes* hybrid was based solely on the description of a pelt bought by an Ohio fur dealer (Bezdek, 1944).

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